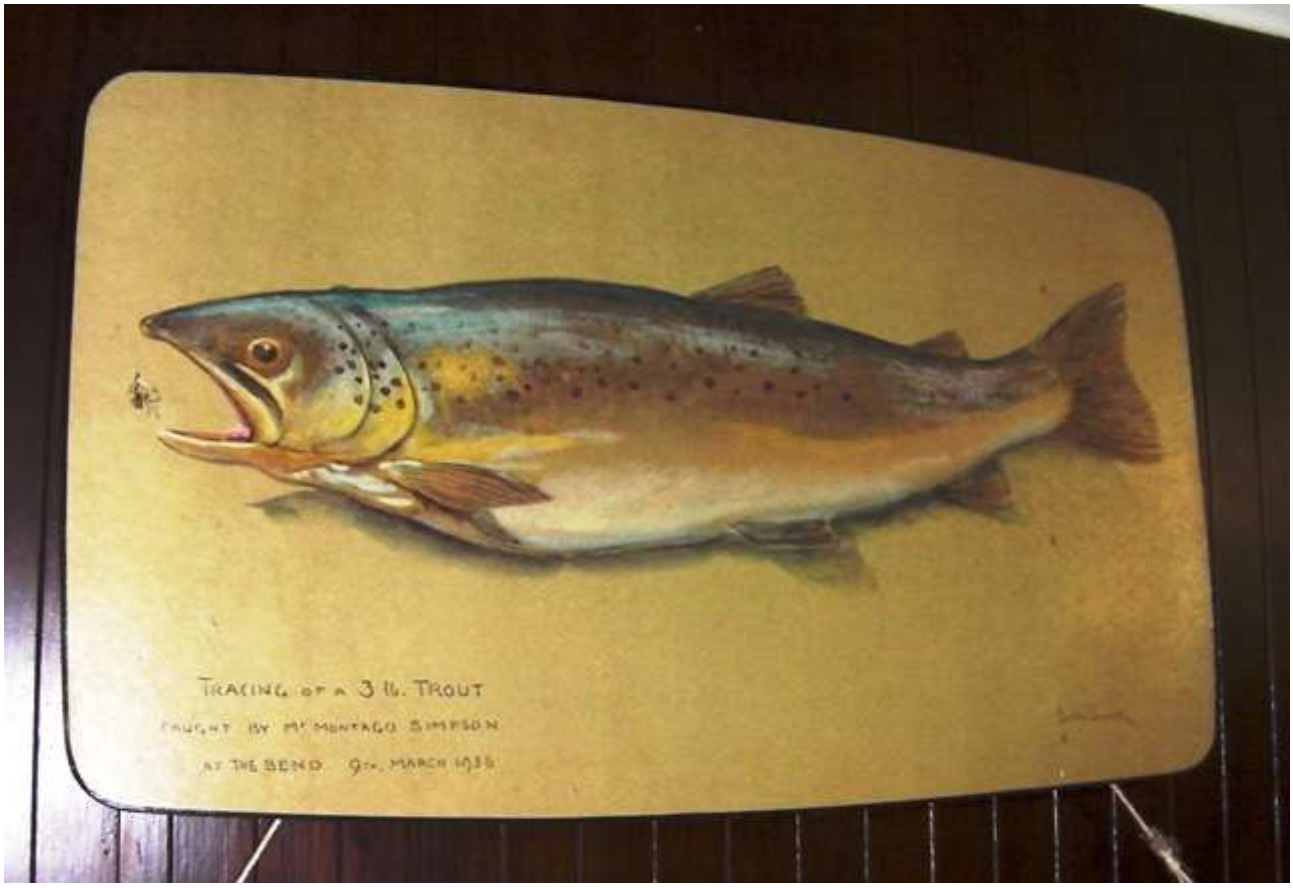
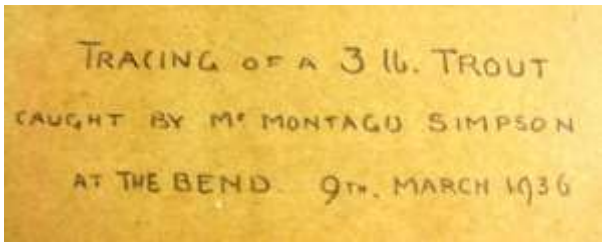
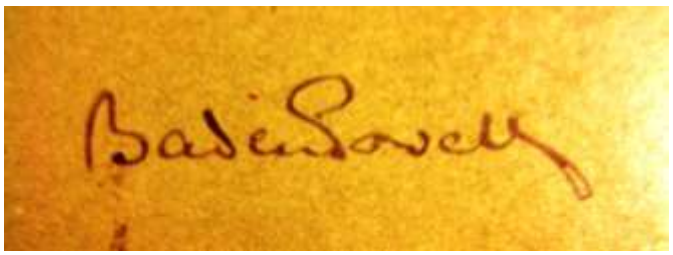
Geographical Factors Affecting the Distribution of Trout in Natal, South Africa.

My rather unsophisticated mini-project submitted in partial fulfilment of my under-graduate degree in the Geography Department at the University of Natal, Pietermaritzburg. At least Bob Crass, the Parks Board Fisheries Officer gave it his stamp of approval – see the last page.







This is a copy of a painting done by Lord Baden Powell and mounted for me by my loving mother, Noelle Margaret Peckham (nee Little). The farm, "The Bend", is on the Mooi River in Natal, South Africa.

SOME ASPECTS OF THE EFFECTS OF TEMPERATURE ON TROUT

WITH PARTICULAR REFERENCE TO NATAL

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JULY 1971

Submitted as an intergral part of
the Bachelor's Degree course in the
Dept. of Geography,
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PREFACE

The general aim of this essay is, as indicated in the title, to investigate some of the effects of temperature on trout, with special reference to the situation in Natal.

It must be realised that almost exhaustive research has been carried out on trout, which rank as one of the most closely studied fish in the world. This leaves little room for original research, especially at third year level, yet although most facts concerning trout under experimental conditions are known, there remains enormous scope for study in a regional sphere. Many writers have taken advantage of this and have produced volumes of literature on various aspects of trout in many different streams and areas. These efforts are not necessarily to be taken lightly since they include some veritable bibles of knowledge and fact, such as Allen's book "The Horokiwi Stream".

It is intended in this essay to consider the known experitmental effects of temperature on trout, to show their dependence on interelated factors and to relate the general conclusions to the situation in Natal, especially when this situation differs from that in the trouts' original northern hemisphere environment. This approach may not, in all cases, be apparent. For instance, it is stated quite categorically that trout die at temperatures of less than $0^{o}C$. This statement does not refer to experimental evidence or to evidence from the field, let alone to any specific reference of the situation in Natal, but this is only because it is abundantly clear that this effect is unlikely to be modified by any environmental situation.

Problems encountered were many. The worst were that much of the literature was almost impossible to come by and many workers, whose results were available, disagreed, or were the result of varying degrees

of accuracy and differing experimental or environmental situations. See Table III for an example. This led to difficulties in interpretation and some conclusions were of necessity arrived at by resorting to sifting out of the more significant figures on no more than an intuitive basis. Another problem which recurred frequently was that figures for many significant factors in Natal were not only unobtainable, but in many cases were non existant.

In Section B for example, it would be deemed essential to provide an isotherm map, average water temperature map and an isopleth map of silt contents, yet maps of suitable scale were unobtainable.

Section B is only indirectly related to the topic, but no apology is offered for its inclusion because of its significance as discussed in the introduction.

A figure given without a source reference indicates that it is original and is not taken from any book. Its derivation is developed in the text.

Details of publications of writers mentioned in the text are marked with an astirisk and are given in alphabetical order in the bibliography, which also includes references not mentioned specifically in the text.

My thanks go to Mr R.S.Crass, Senior Fisheries Research Officer of the Natal Parks Board who provided much in the way of literature and advice and to Mr Fitzpatrick whose advice on the presentation of this essay was extensive.

A. INTRODUCTION

Temperature is a major factor influencing the livelihood of trout, as subsequent sections will show. It is, however, crucial to bear in mind the fact that temperature is only one of many factors which range from vitally significant ones of broad scope, such as conservation in catchment areas, food resources and temperatures, down through a gradation to a multiplicity of less significant factors including, for example, shading provided by marginal vegetation, predation by otters and competition with scalies (Barbus natalensis).

It is the complex interaction of these factors which determines the exact conditions of a trout's existence and it is obvious that such a range of variables in differing proportions gives rise to an infinite number of possible combinations. It is thus necessary when considering any specific set of circumstances, to hold complimentary factors fixed at some arbitarily suitable level. It is not impractical or unrealistic to do this as long as it is continually borne in mind that the final result of the aspect being considered may well be overshadowed by infringing factors. At this stage one can pronounce one's results results ceteris paribus,, or proceed to analyse the modifications which might arise from such an infringement.

This is all very general, but the object of Section B is to give an indication of the manner in which the interactions of selected factors, influences the spacial distribution of trout in Natal, so that subsequent sections, devoted almost entirely to effects of temperature, can be seen in perspective.

There is absolutely no attempt at undertaking a comprehensive analysis of factors influencing the distribution of trout and Section B is aimed simply at reinforcing the general ideas expressed above, whilst relating them to a concrete example.

Section C is the body of this essay and tackles the problem as laid out in the essay's title. It categorises the effects of temperature on trout in to sub sections distinguished on a basis of the stage of the life cycle. It is those effects of temperature on trout, which are not conclusively established, that are considered most fully.

There is no concluding section because the summarising paragraphs at the end of each section or subsection serve collectively as a conclusion and have the added advantage that the conclusions are discussed immediately after the relevant section. This helps to crystallise the ideas in each section, as they are presented.

B. THE INTERELATION OF SOME FACTORS WHICH INFLUENCE THE DISTRIBUTION OF TROUT IN NATAL.

According to Hesse (1937) important factors influencing trout and their food pyramid are the velocity of stream flow and stream gradients, the nature of the substratum, hydrothermal conditions and the varying gas contents of the water. The effects of various factors which limit the distribution of trout in Natal will now be considered.

One might first consider the effects of stream gradients (See Table I).

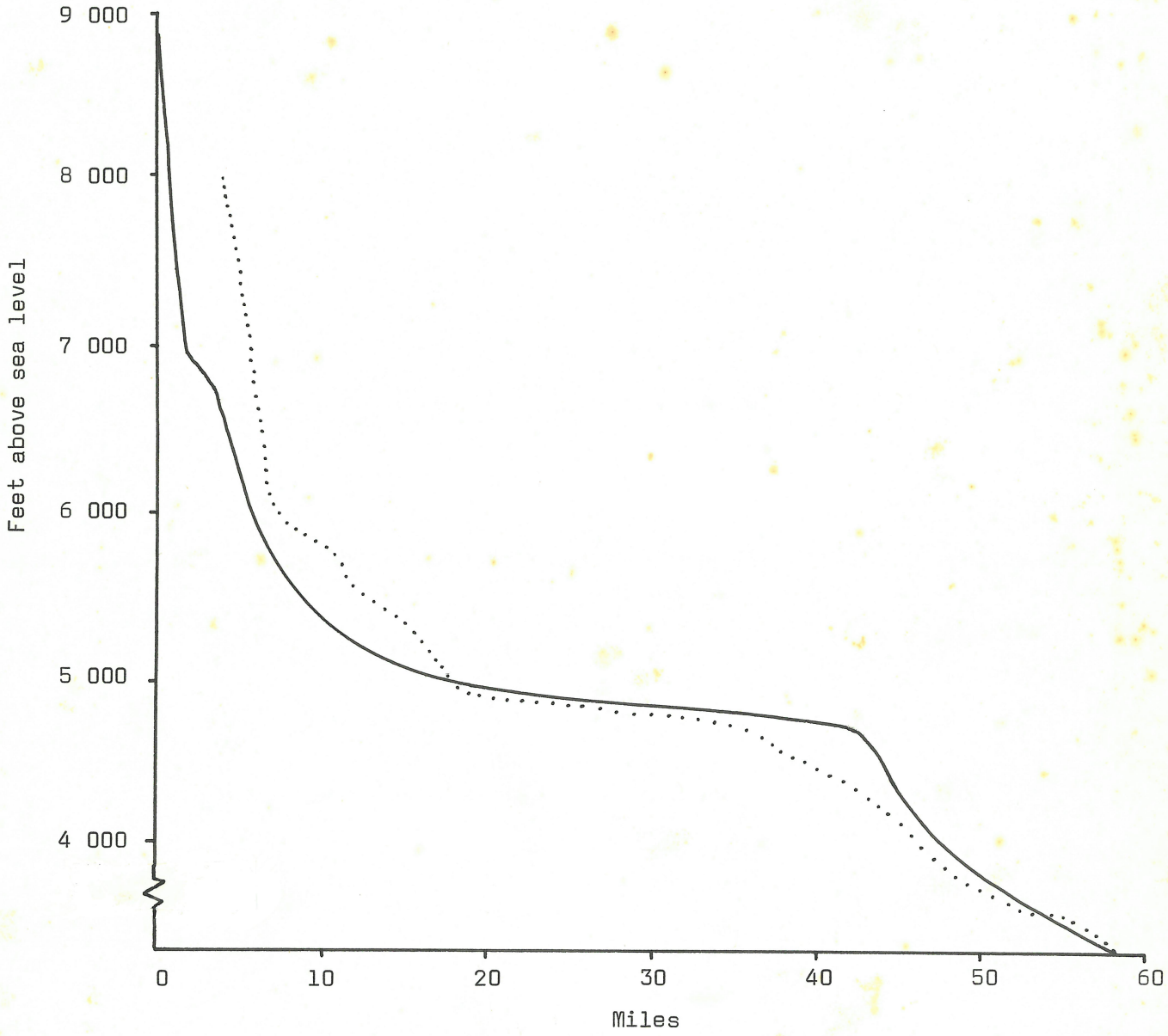
TABLE I : The average gradients of some streams in trout and troutless zones expressed as feet per mile

Stream	Average gradient in trout zone	Average gradient in troutless zone
Umzimkulu	104	29
Polela	88	29
Ingangwana	55	26
Umkomaas	111	25
Loteni	68	25
Mooi	80	22
Bushmans	114	21

Source : Natal Parks, Game and Fish Preservation Board records.

The table shows that the gradients in the trout zones are all above 55 feet per mile whilst the highest gradient in the troutless zone is only 29 feet per mile. The significance of the correlation is immediately queried, since it is well known that trout can survive in both lotic and lentic environments and a more detailed comparison shows sections of rivers within the trout zone which have very low gradients yet which carry thriving trout populations. Examples of this phenomena are abundant. Consider for instance the marshy section on the upper Inyamvubu and the sections on the Umzimkulu and Polela

Figure 1 : Profiles of Polela and Upper Umzimkulu Rivers.



KEY _____ Umzimkulu

..... Polela

V.E. = 53 X

SOURCE Parks Board Records

which lie between 4 700 and 5 000 feet (See Figure 1). These stretches of river have gradients of less than 15 feet per mile.

Conversely, there are as many cases of sections of rivers with a steep gradient which do not support a population of trout. Although the gradient is steep, there are no trout in the Oribi Gorge section of the Umzimkulu, for example, mainly because water temperatures and silt contents are too high.

It is apparent then, that whilst gradients may influence the distribution of trout, there are certainly other factors which modify its effect. The most important of these factors would probably be water temperatures and silt suspensions, as mentioned above and if detailed information were available[1] for water temperatures and silt contents then from existing knowledge of the extensive effects of these factors on trout, it would be expected to find a correlation, and probably a very close one, between either of these factors and the distribution of trout, but deviations from the expected distribution would exist, and these deviations could be accounted for in terms of modifications arising from various infringing factors. This type of reasoning shows up well considering the relationship between rainfall and trout distribution (See Figure 2).

Rainfall has only a limited direct effect on trout, but indirectly it exerts an extensive influence. The inland high rainfall areas are usually cooler. They usually occur in hilly areas which means that streams are quick flowing, well aerated, have an eroding and gravelly substratum and high rainfall areas more often than not, occur in areas

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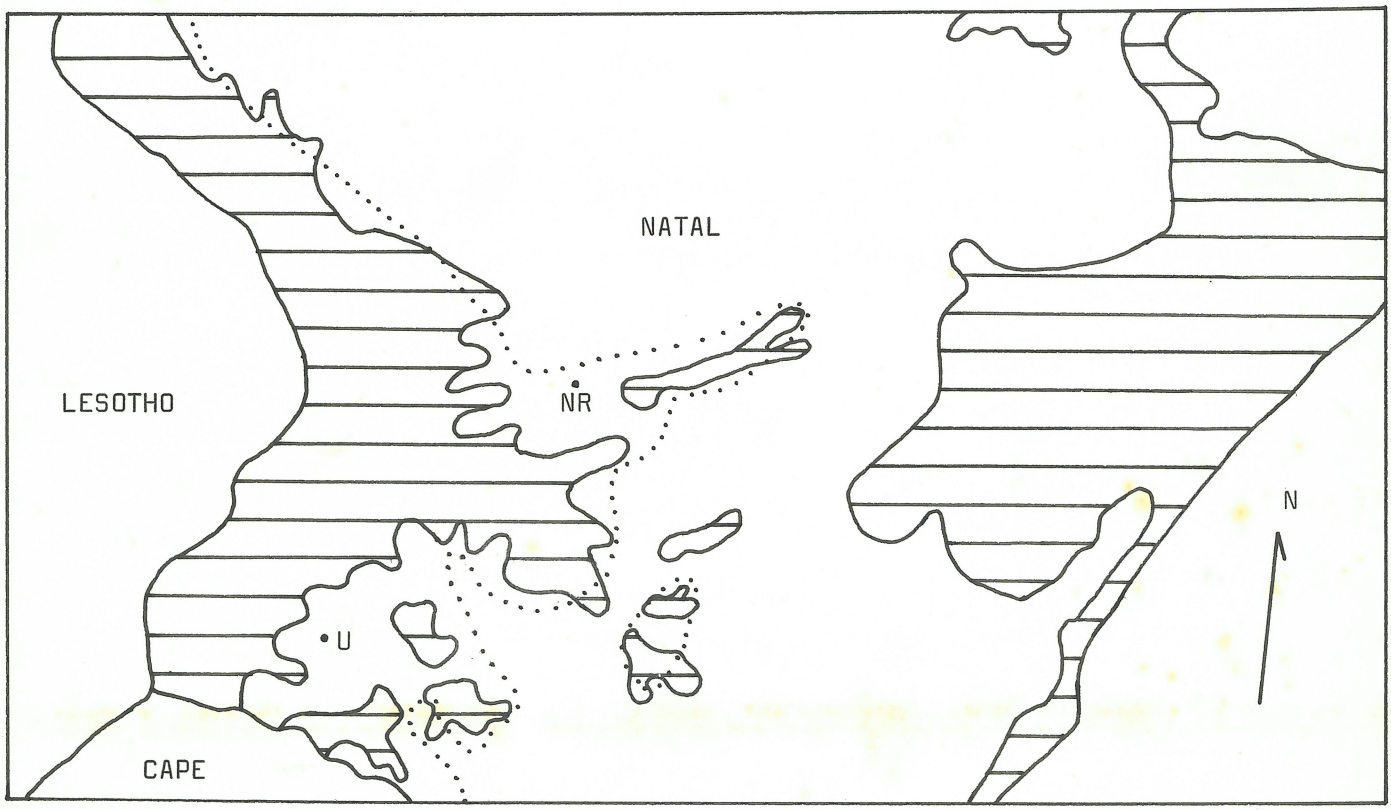
[1] Statistics for silt contents and water temperatures are available for many of Natal's rivers, but these are recorded at various measuring stations and give isolated "spot values" whereas it is only figures for the change in silt content and water temperature along the river's course, which can be of any value in this case.

Figure 2 : The correlation between the 40" isohyet and the eastern limit of trout in Natal.



KEY — Areas receiving a rainfall of more than 40"

..... Eastern limit of trout

U Underberg

NR Nottingham Road

SCALE 1:1 500 000

SOURCE McKenzie (1948) Crass (1964)

which are better conserved. This leads to improved clarity and greater stability of stream flow with less seasonal variation. Each of these factors affect trout, both supplementary to other factors and independently. This gives an indication of the extent of the influence of rainfall.

Since rainfall has little direct effect on trout one would not expect much correlation between trout and rainfall distributions, but it is the wide range of other factors which interact with rainfall, as discussed above, which accounts for the very close correlation between the eastern trout limit and the 40" isohyet.

There are only three major deviations from the 40" isohyet. These are the area around Underberg, the large area along the coast and the region to the east of Nottingham Road. Of these, only the first two are of any significance.

The Underberg area suffers from the rainshadow effects of a ring of surrounding hills especially in the south and east. This may lower the rainfall over this particular section of the Umzimkulu but it is unlikely to have any significant effect on the stream flow, since the upper and lower sections of the river and all the important tributaries flow from high rainfall areas. This lends stability to the stream flow through the dryer Underberg valley section.

The area along the coast, like all low lying areas in Natal has water temperatures and silt suspensions which are too great for the survival of trout. Hence there is a total absence of trout in this region[2].

The area to the east of Nottingham Road contains many of Natal's most productive trout dams. The region does have a rainfall of less

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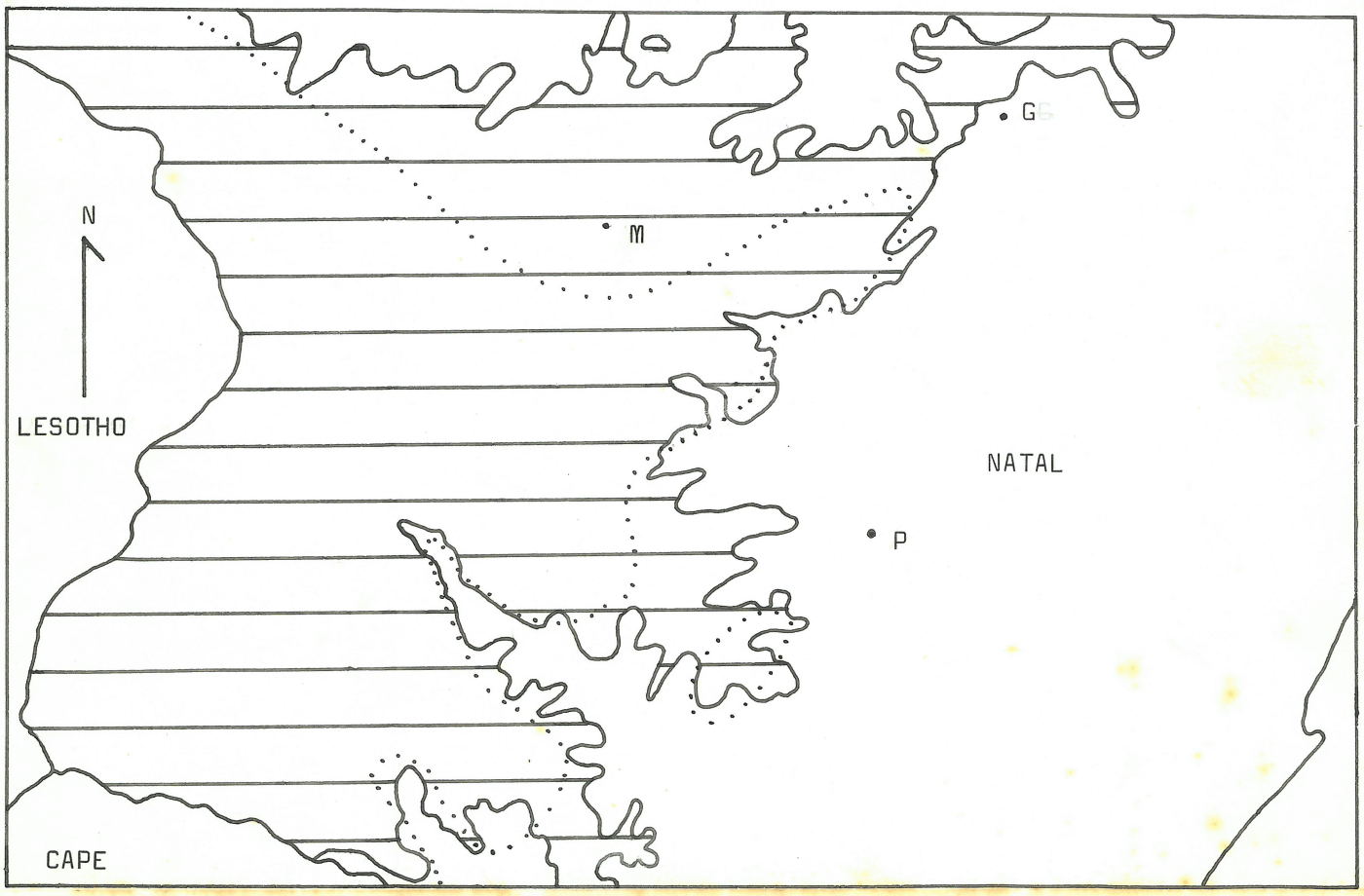
[2]The only exception at present is the one mentioned on page 6.

Figure 3 : The correlation between the 4 000 foot contour line and the eastern limit of trout in Natal.



KEY	Areas over 4 000' a.s.l.
.....	Eastern limit of trout
P	Pietermaritzburg
M	Mooi River
G	Greytown
SCALE	1:1 000 000 (approx)
SOURCE	Crass (1964)

than 40" but this is of little consequence since the 35" isohyet, (not shown in Figure 2) runs well to the east of the trout limit indicating that this area does in fact have a rainfall close to 40" and thus ruling out the significance of the deviation.

The 4 000 foot contour line and the trout limit also show a close correlation (See Figure 3). Many of the smaller apparent deviations exist simply because there are no streams flowing in the locality which are sufficiently large to carry a trout population. Thus, when the lower limits on two trout streams are joined with a smooth curve, a valley of less than 4 000 feet or a spur of more than 4 000 feet may be cut off[3], whereas if a stream was situated here one might well expect the limiting curve to follow the 4 000 foot contour line more closely. This idea holds true for Figure 2 as well.

The only notable deviation from the 4 000 foot contour is the one to the east of the trout limit in the Mooi River - Estcourt district. This region boarders the dry interior of the Tugela valley and falls in the rainshadow of the Karkloof range so that rainfall in this region is low, whilst temperatures and silt suspensions are high, causing the area to be unsuitable for trout.

Mention must be made of the establishment of trout in Zululand, near Eshowe at an altitude of only 1 600 feet. These trout have been stocked in a dam on Mr L.Gunter's farm. The dam is fed by a stream which rises in a heavily wooded valley in the Ngotshe forest and which is consequently cool and clear. A maximum temperature of 25°C was recorded in 1968 when the air temperature rose to 42°C but at a depth of three metres the water temperature was only 19°C and well within the tolerance

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[3] For example the spur through Greytown (Merthley Lake was a productive trout dam at one stage and attempts are being made to restock it) and the one through Donnybrook.

limit for trout[4]. Reed covers have been constructed around the edge of the dam to provide shade and to prevent the water temperatures in the shallows from rising excessively.

Survival of trout in this oasis can be attributed to the strong continuous flow of 1.5 cusec of cool well aerated water from the feeder stream and to the restriction of temperature rises by the use of shade covers. Similarly suitable conditions may exist in other isolated and very localised spots, but getting back to Figure 3, it is found that the reason for the close correlation between the 4 000 foot contour line and the trout limit, is an interplay of factors similar to that mentioned for rainfall; high lying areas are cooler on the whole, they intercept more rainfall have better head water and catchment area conservation, steeper gradients, and all the related implications of these favourable factors.

A Parks Board publication "Trout Farming" suggests that the factors which must be considered when determining the suitability of water for trout, are the relationships between water temperatures, gas contents, turbidity, mineral content and freedom from pollution.

The overall conclusion reached, is that the trout limit corresponds to an adaption of Liebig's Law of the Minimum, viz. that the distribution of trout is ultimately restricted by that habitual factor which most approaches the minimum requirement. Crass (1964) comes to the conclusion that it is usually the occurence of too large a silt suspension which is the primary factor limiting the spread of trout in Natal's streams since silt concentrations frequently become unsatisfactory before temperatures or other factors reach inhibitory levels.

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[4] Trout can survive maximum temperatures of about 28°C.

This covers the interelationship of some factors which affect the distribution of trout in Natal. The general effects, on trout, of one of these factors - temperature is now discussed.

C. SOME EFFECTS OF TEMPERATURE ON TROUT.

Given food temperature becomes possibly the single most dominant factor governing the existence of trout and influencing many aspects of their life from spawning and hatching through to their ultimate death.

(i) Spawning and Hatching

Most sexually mature trout spawn every year, in winter. Brown trout[5] spawn from mid May to mid June and rainbow trout from early June until late July. They start moving upstream in autumn, in search of gravel beds suitable for spawning.

The upstream migration is caused mainly by the breeding urge, resulting from biological factors such as the ripening of the reproductive organs and the secretion of gonadial hormones, but it is generally agreed by most experts (see following paragraphs) that some external factor provides the final stimulus to the migration.

Van Sommeren (1952) working in Kenya came to the conclusion that the final upstream migration is stimulated by the dilution of streams by flood waters, and Frost and Brown (1967) quote many examples in the U.K. where, migration coincides with an increase in the volume of stream flow. This theory is unlikely to apply rigidly in Natal since there is fairly consistant decrease in stream flow during the crucial period (See Figure 4).

More applicable is Stuart's (1953) theory. He found that the

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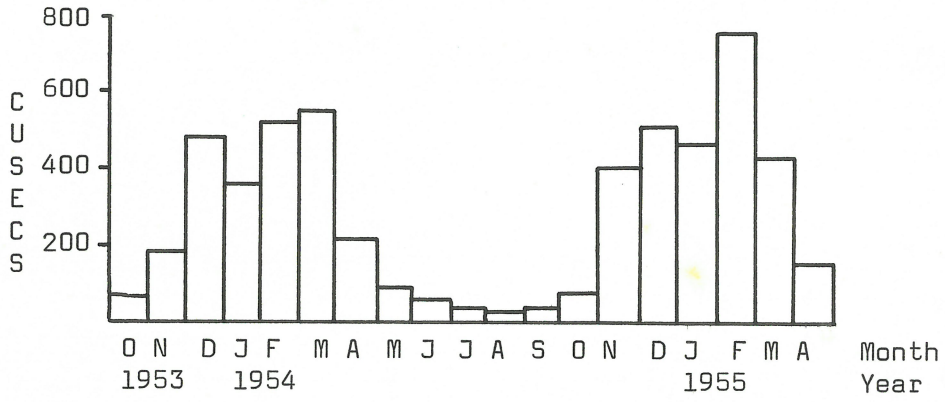
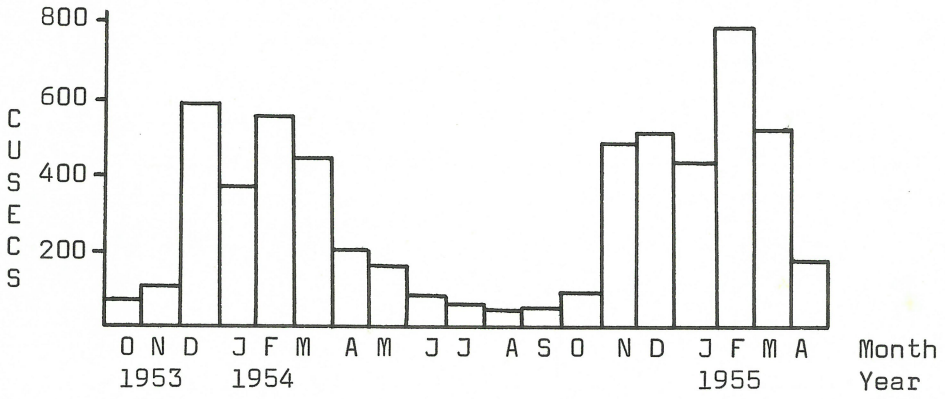
[5] Only two species of trout occur in Natal. These are the brown trout, Salmo trutta, and the rainbow trout, Salmo gairdneri. The American eastern brook trout, Salvelinus fontinalis, was introduced in 1953 but failed to become established and has died out.

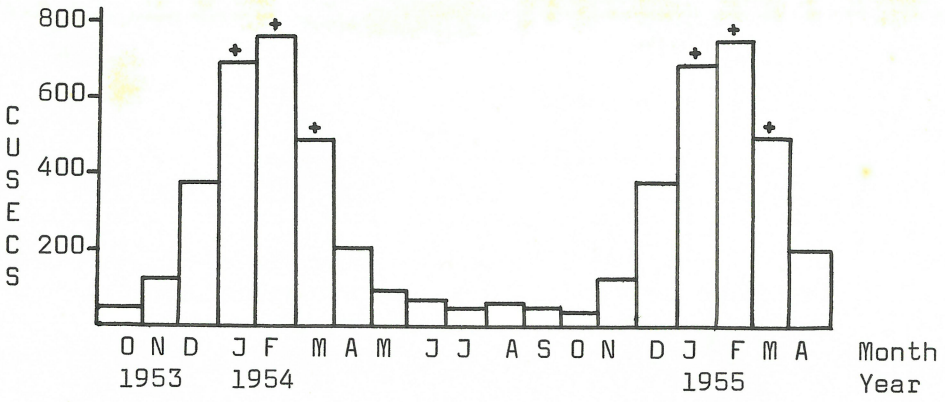
Figure 4 : Mean monthly flow rates of some trout streams in Natal.



Malambonjwa River, gauging weir number 387.



Bushmans River, gauging weir number 211.



Mooi River, gauging weir number 401.

+ indicates that the weir was submerged. (Highest recorded value is given)

SOURCE Oliff, W.D. (1960)

final upstream migration which immediately precedes spawning, was temperature dependant and that trout in Scotland began the migration when the water temperature had dropped to 7°C. Later the effects of acclimatisation to temperatures, by trout will be discussed, and in view of this it would be expected to find a higher temperature operating in Natal, corresponding to Stuart's 7°C. Figures are, however, unobtainable.

The temperature theory is lent support by the behaviour of trout in Kenya, which is on the equator and which, therefore, has negligible seasonal temperature fluctuations. These trout have no specific breeding season and some ripe trout are caught each month. This suggests that in Kenya, since there is an absence of a seasonal, country-wide temperature drop, trout do not spawn at any specific time of the year as they do in the poleward countries which experience a temperature drop as winter approaches.

Referring back to the flood theory, it is immediately realised that since flooding almost always reduces the water temperature there is no real disagreement between the two points of view and it is temperature, after all, which is the stimulating factor. The only significant difference between the ideas of Stuart (1953) and van Sommeren (1952) is then reduced to the fact that whilst Stuart's observations lead him to believe that the migration corresponded to a specific temperature value, van Sommeren and Frost and Brown indicate that it is stimulated merely by a temperature drop at a suitable period in the reproductive cycle.

This conclusion is far more logical since trout eggs only survive at low temperatures, so that a ripe trout would instinctively spawn, if possible, when temperatures dropped, so as to try and ensure a successful hatching.

By Stuart's more dogmatic approach one might well be faced with the situation in which an unripe trout would have to hurry upstream to spawn, simply because the water temperature had now dropped to the critical 7°C level.

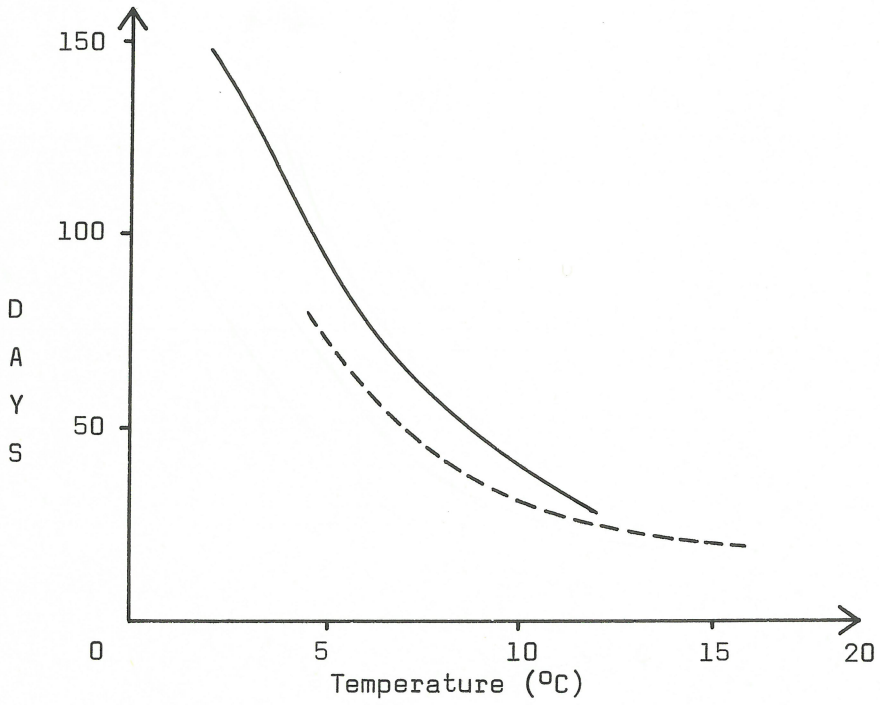
A temperature drop then will definitely stimulate upstream migration, provided it occurs whilst the trout are ripe, but it is not the most vital prerequisite, the stage of the reproductive cycle being dominant.

An example of such a migration occurred in Lake Lyndhurst but an explanation is first required. Trout cannot breed in dams, only in running water. However, trout stocked in dams still mature and experience the breeding urge, but can only spawn if a suitable stream feeds the dam. If there is no stream available the trout become spawn bound and the eggs begin to deteriorate within the body cavity.

Now Lake Lyndhurst, on the upper Umgeni is fed only by this stream and by another small feeder stream. Trout in the dam ripened in the winter of 1970 but could not spawn because the feeder streams were too small to negotiate safely. However, in the last days of August, after the end of the usual breeding season, several inches of rain fell, decreasing the water temperature and increasing the volume of the stream flow to a level at which the fish could enter the stream. Hundreds of trout promptly migrated upstream to spawn. Had it not been for the increase in stream flow, the trout would not have ventured into the stream and no breeding would have occured.

It can be argued that an increased stream flow would stimulate migration only because it enables the trout to swim up through shallow rapids and riffles more readily. This idea would certainly have applied to some extent in the example above but it does not explain why trout in rivers with an ample depth of water still migrate when the river flow increases.

Figure 5 : The change of the incubation period of trout eggs with temperature.



KEY _____ Brown trout eggs

----- Rainbow trout eggs

SOURCE Embody (1934)

Both ideas[6] probably operate simultaneously to some degree the dominating one being dependant on the particular circumstances.

After the spawning migration the eggs are laid, fertilised, covered with gravel and then deserted. Temperature now plays a delicate role. Frost and Brown (1967) quote a figure of 13°C as the maximum temperature which fertilised eggs will withstand, provided that the oxygen content of the water is sufficient and that no silt deposits accumulate. Both of these factors are facilitated by a circulation of cool water through the gravel substratum in which the eggs are deposited.

In Natal, trout are accustomed to higher temperatures and Crass (1964) found trout eggs survive up to a temperature of 15½°C. Since spawning occurs in winter trout eggs in Natal are very unlikely to encounter temperatures exceeding this value and spawnings in most streams are very successful. So much so, that many rivers are grossly overstocked.

The incubation period for trout eggs shows an inverse correlation to the temperature (See Figure 5). These graphs are based on work done by Embody (1934) in the U.S., and agree very well with the figures of forty-two and thirty-six days, for brown and rainbow trout respectively, at 10°C, which Crass (1964) gives as typical values for trout eggs in Natal's streams.

This sub section, then, concludes that a drop of water temperature will stimulate a spawning migration provided the trout are ripe and that the incubation period of both brown and rainbow trout eggs is shortened as temperatures rise.

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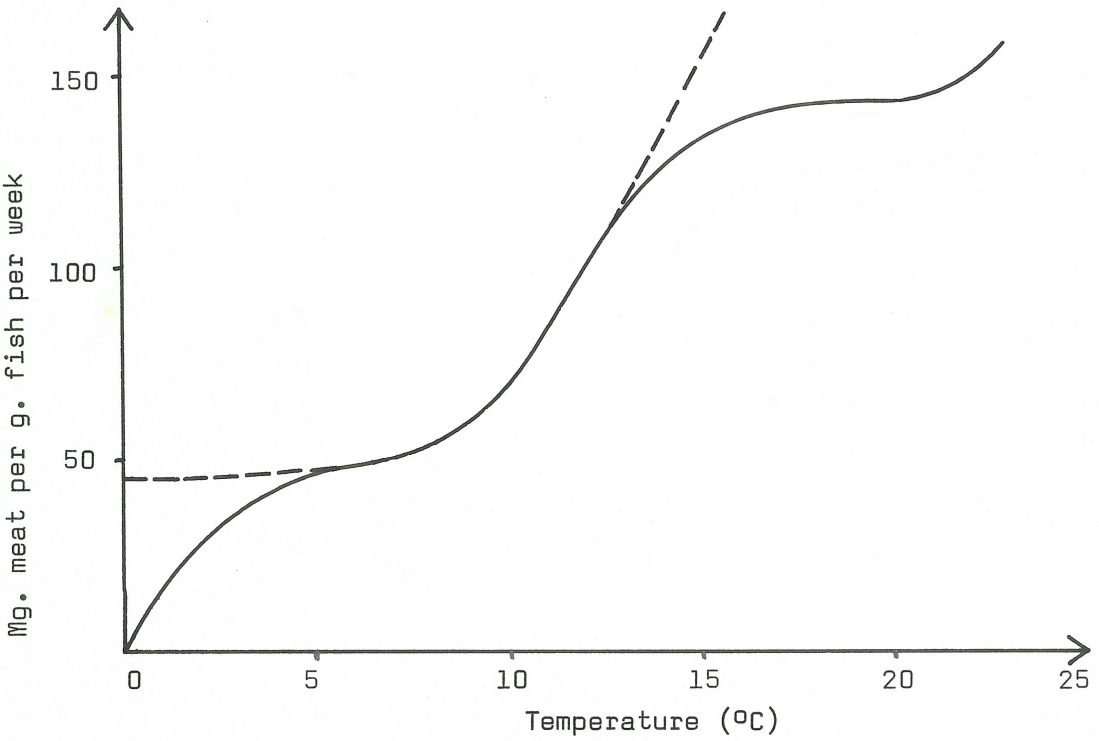
[6] (i) That a temperature drop, whether it occurs with an increase of stream flow or not, stimulates migration.
(ii) That an increased stream flow stimulates migration by enabling the trout to negotiate the stream more easily.

Figure 6 : The variation of maintenance requirements of trout with temperature.



KEY ——— Maintenance requirement

----- Expected curve

SOURCE Brown (1946)

(ii) Growth

The predominant factor influencing the growth of trout, is the interaction of the food supply and the density of the trout population which it supports (See Figure 11). Temperature played a significant but limited role in the last sub section whilst in this sub section it holds a less significant but more extensive sway.

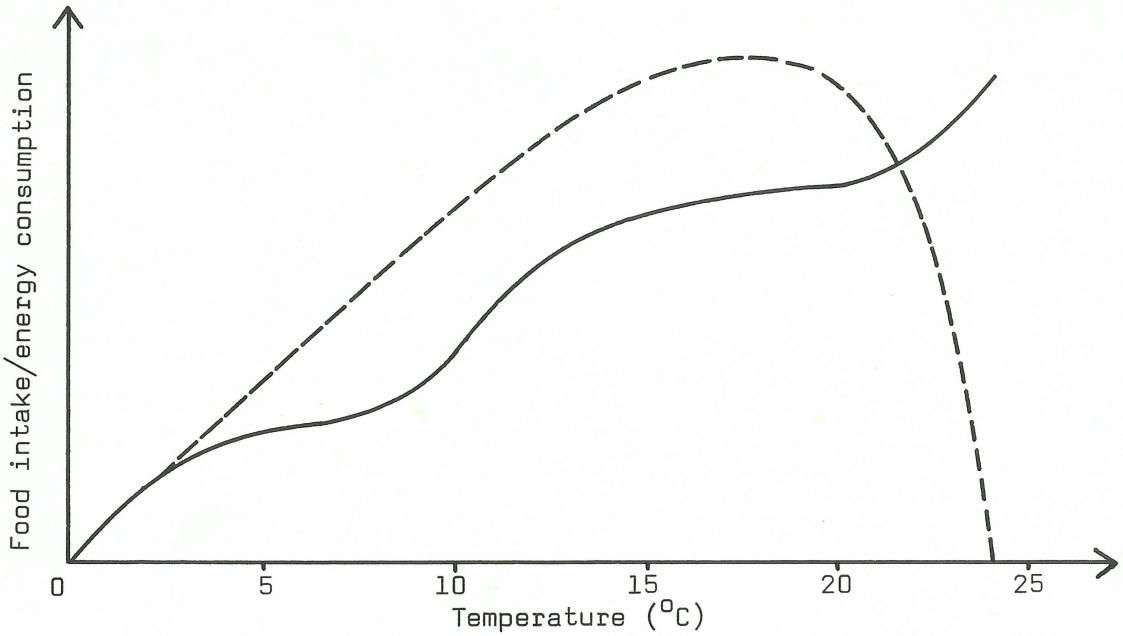
Every animal uses up a certain amount of energy, simply for the processes involved in staying alive and therefore requires a certain amount of food as a source of this energy. An equilibrium between food intake and energy expenditure leaves no room for growth, and on this basis the maintenance requirement for a trout is defined as the quantity of food required to just keep it at a constant body weight.

In view of this, it will be readily appreciated, that the maintenance requirement for trout could be freely interpreted as its energy expenditure. This argument enables one to interpret Brown's (1946) maintenance graph (See Figure 6) as a graph of the energy expenditure of trout as the temperature rises.

One would expect the graph to increase exponentially with temperature (Brown 1946). (See dotted line on Figure 6). The reason why it deviates into an S shape is probably due to the fact that trout become less active as the temperature extremes are approached (See Figure 13) and since normal bodily activity is taken into account in the assessment of maintenance requirements we would expect the maintenance requirement to fall off with a decrease in activity.

This curve is redrawn in Figure 7, retaining its characteristic shape, but abandoning the units which would otherwise restrict it to a specific case. The only other difference is that the graph is now referred to as an energy expenditure curve as discussed above, and not as a maintenance requirement curve.

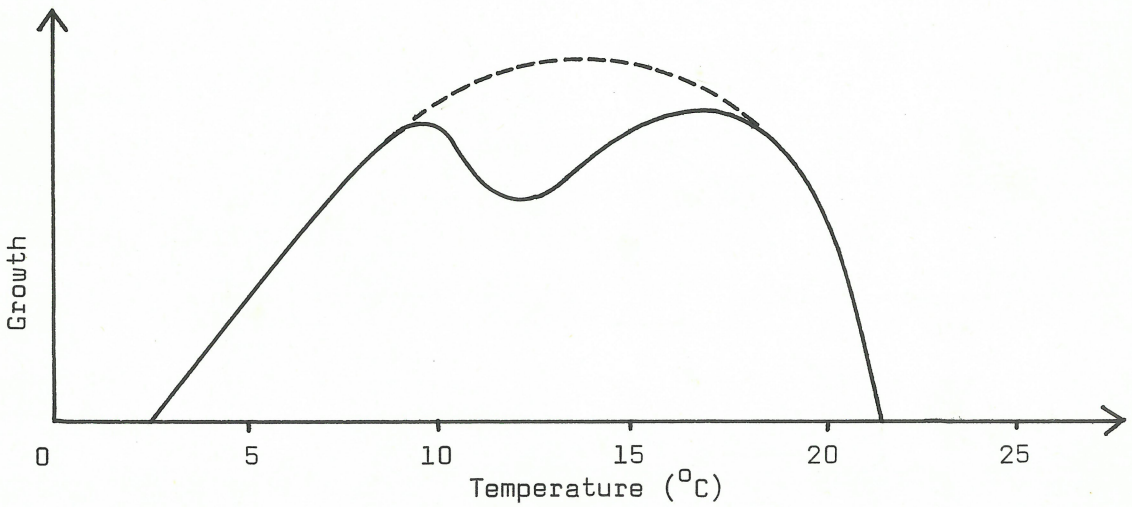
Figure 7 : The food intake and energy expenditure curves for trout, as a function of temperature.



KEY _____ Energy expenditure curve

----- Food intake curve

Figure 8 : Change of growth with temperature as derived from figure 7.



V.E. = 2 x that on figure 7

KEY _____ Actual growth curve

----- Expected growth curve

The food intake curve in Figure 7 is to some extent intuitive and is based on the following observations :

(a) The food consumption curve must start from $0^{o}C$ since at this temperature there is no energy output or food intake, the trout being dead. (Maciolek and Needham 1952). This provides an accurate intercept at the origin.

(b) Trout can survive temperatures close to freezing but do not grow under such extreme conditions. (Frost and Brown 1967). It has been explained that a lack of growth indicates that food intake balances energy output, and this accounts for the section over which the two curves coincide.

(c) Food intake improves as temperatures increase, up to a maximum in the region of $18^{o}C$. (McAffee 1966) (Crass 1964). This determines the lateral position of the maximum (the vertical position depends on the arbitary Y-axis units).

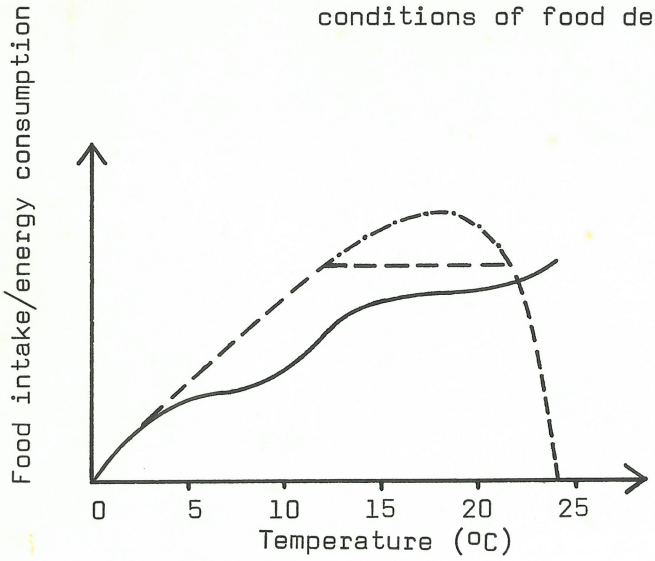
(d) Trout continue to feed up to at least $24^{o}C$ (Crass 1964). At a few degrees higher they die anyway, so this X intercept is also fairly accurate.

These four factors account for the shape of the food intake curve.

It has already been explained that growth corresponds to the excess of food intake over energy expenditure so that in Figure 7, growth is represented by the area between the two curves. The difference between the curves has been plotted to give a curve (See Figure 8) for the change of growth with temperature. It must not be forgotten that whilst Brown's (1946) curve, (Figure 6) was one of finite values, figures 7 and 8 represent only the relative values derived by the above discussions.

It has been shown experimentally and in practise on some rivers to the angler's frustration, that trout have a definite limit to their appetite, and if a surplus of food exists, they will only continue

Figure 9a : Food intake and energy expenditure curves under conditions of food deficit.

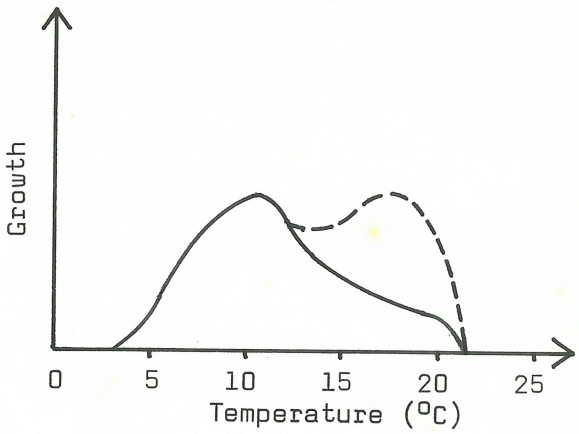


KEY _____ Energy expenditure

----- Food intake under conditions of food deficit

-.-.- Food intake under conditions of food surplus

Figure 9b : Growth curve derived from figure 9a.

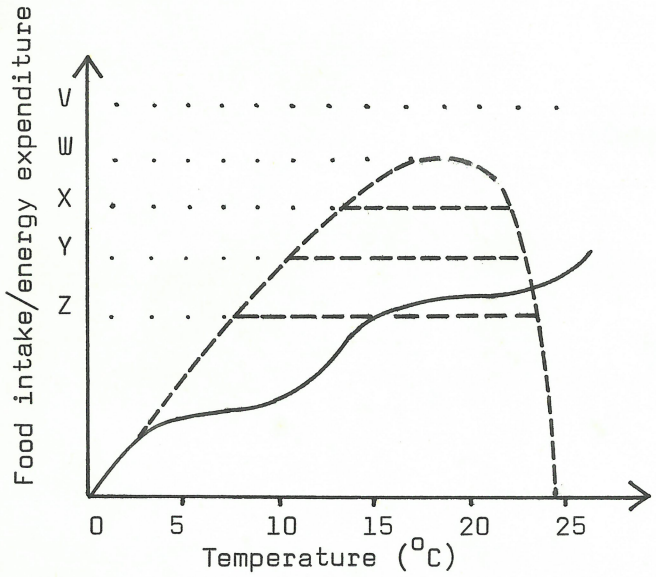


V.E. = 2 x that in figure 9a.

KEY _____ Actual growth curve

----- Expected growth curve

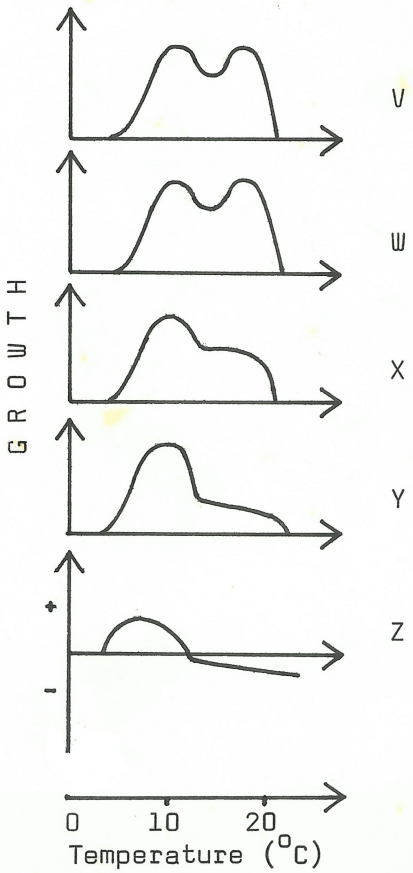
Figure 10a : Summary of different food/energy curve situations.



KEY _____ Energy expenditure

----- Food intake under various conditions of food surplus and deficit

Figure 10b : Resultant growth curves from figure 10a.



feeding up to some specific level. If, however, the food supply was insufficient, the trout would consume all the food available and this would produce a flattened section in the food intake curve, corresponding to the maximum food supply available (consider Figures 9 and 11 together).

Under conditions of a food deficit, an increased amount of food, which has the same effect as a decrease in the trout population, would have the effect of raising the plateau section and thus giving rise to a greater growth at temperatures in this region (consider Figure 10 changing from Y to X).

Consulting Figure 11 it is seen that trout with a surplus food supply fall into area A. At C trout have just sufficient food to satisfy their appetites. These situations correspond to figure 10 at the V and W positions respectively which both give identical growth curves since the trout can feed to capacity in each case. However, the situation at B in figure 11, where there is a varying degree of food deficit, gives rise to growth curves represented in figure 10 by X and Y. In contrast with a food surplus situation, a food deficit can show a great variety of growth curves - intermediate situations between W in figure 10 and no growth at all.

The food deficit situation is probably the most realistic for Natal's streams which are mostly overstocked. An interesting implication of the food deficit situation is that growth is less at higher temperatures than it is in the region of $8^{o}C$. Such low temperatures do not occur in Natal streams during the summer growing season and it would be interesting to establish if trout would in fact grow faster at lower temperatures under conditions of restricted food supply, in contrast with the common opinion that growth improves with temperature.

Figures in support, or otherwise, of this idea are unobtainable, but the idea could be backed up by the argument that at lower temperatures trout would require less food, however, the amount of food available is likely to remain unchanged so that the stage would be reached at which the trout's decreasing appetite would fall to the level of the food available, whilst its energy consumption decreased and its growth rate therefore increased simultaneously.

In practise the plateau section of the food intake curve under conditions of a food restriction should not fall below the energy expenditure line because as the food limit was reached, the trout would stop growing. In fact, this situation can arise when a few good years may allow unusual growth and food supplies may then be reduced by a flood or drought stricken year, in which the now large trout are unable to find sufficient food. Such fish would lose condition and the growth curve would fall below the zero level (Figure 10, situation Z).

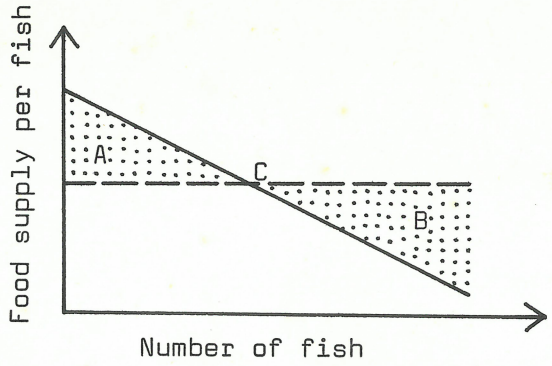
It is important to understand the difference between absolute growth and growth rates. An example will make this clear. If a four year old trout was weighed in at say four pounds then it is quite likely that its weights at the end of each successive year would be $1\frac{3}{4}$lb., 3lb., $3\frac{3}{4}$lb., and 4lb[7] so that its growth <u>rate</u> decreased with age. Conversely a four year old trout of a pound may have weighed $\frac{1}{4}$lb., $\frac{1}{2}$lb., $\frac{3}{4}$lb., and 1lb., at the end of each year[8]

---

[7] This is realistic since a limited food supply is unlikely to expand to meet a trout's increased requirements as it grows larger.

[8] This would apply only when food supply exceeds the demand of the trout population, and the small annual increment to weight in this example could be attributed to factors such as very low temperatures which would inhibit feeding. Trout in understocked dams and newly stocked rivers also show a regular growth rate, but at a higher level, usually, than $\frac{1}{4}$lb., a year. (<u>NOTE</u>: Trout breed only in running water so that an understocked dam remains understocked, but in an understocked river, the population soon builds up as densely as the food supply will allow).

Figure 11 : The relation of food supplies to the density of the trout population.



KEY ----- Food intake limit per fish ie. maximum appetite

_____ Food available per fish as numbers increase

A Surplus food not exploited by trout

B Food deficit which trout would exploit if food became available

C The equilibrium and optimum position

Figure 12 : 3D depiction of a decreasing growth rate.

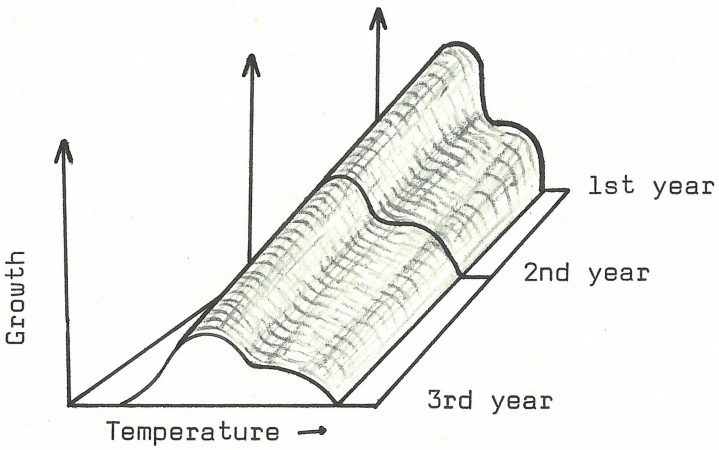
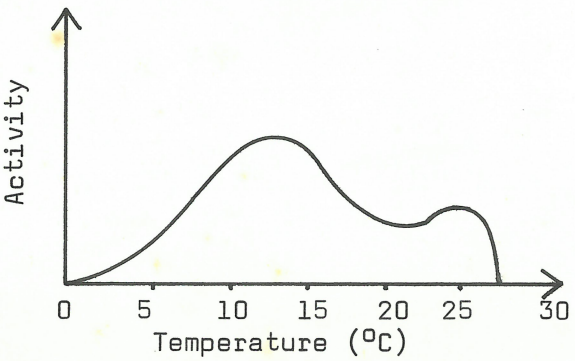


Figure 13 : The activity curve for trout as a function of temperature.



SOURCE Data from Dill and Soule (1948) and Frost and Brown (1967)

Here, the smaller trout had a higher growth rate. The point is that growth rates may be quite unrelated to actual size, that is to absolute growth.

However, in view of the last two footnotes and the fact that in Natal it is the food barrier which limits growth, it can be said that on the whole large trout are large only because they have a high growth rate and one can speak of growth and growth rates interchangeably as long as one is aware of the difference.

In terms of figure 10, actual growth would be shown by the (b) sections whilst to imagine growth rates, one would have to consult successive diagrams for each year of a trout's life. Then, as the trout grew, its energy consumption line would rise towards the food limit line (X or Y in figure 10a) and successive values for growth would decrease, indicating the decreasing growth rate (See Figure 12).

This covers the derivation of the figures relating to growth and a discussion of the various possibilities which would be expected to arise. Some of the experimental evidence can now be considered to see whether there is any agreement between these derived figures and actual findings.

Within a temperature range of 7 - 12^{o}C trout fry from similar sized ova develop at a similar rate, but beyond the limits of these temperatures, development is restricted resulting in smaller fry which usually maintain their smaller size throughout life when compared with larger fry which were not exposed to extremes of temperature.

It has also been found that adult trout can survive temperatures from 0 - 28^{o}C but do not grow successfully at either extreme. Also, trout growth improves as temperature increases up to a debatable optimum of somewhere in the region of 18^{o}C and decreases rapidly as temperatures rise above this.

This improvement of growth is easily explainable on a biolcgical basis; trout are cold blooded and as water temperatures rise so does the temperature of the trout and its metabolic rate increases, including the rate of digension. At higher temperatures then, a trout is able to eat and digest its food more quickly (See Table II) for conversion into energy and body weight. There is, however, a contradictory factor.

TABLE II : The digestion rates of trout at various temperatures.

Food Type	Temp (^{o}C)	Digestion period
Soft bodied organisms	10.5	12 hours
Soft bodied organisms	2.5	25 hours
Hard bodied organisms	10.5	16 hours
Hard bodied organisms	0.5	70 hours

Source : Reimers (1948).

This is the expenditure of energy which also increases as the temperature rises, and opposes the effect of an increased food intake. It has been firmly established experimentally and in the field that a trout's growth improves, with some irregularities as temperature rises so that it can be accepted that the increased food consumption (if the food is available) out weighs the corresponding increase in energy output in most cases. The exception will be mentioned.

These general conclusions have been reached by literally hundreds of workers, each giving slightly different figures for trout in different streams or under different experimental conditions and the set of figures developed earlier in the section ties. in very well with many workers results.

It can be seen from figures 7 and 8 that there is no growth below about 3^{o}C or above 21$\frac{1}{2}^{o}$C. From 3^{o}C growth improves with temperature up to a maximum at about 9$\frac{1}{2}^{o}$C. It suffers a minor setback in the region

of 12°C, then rises to another maximum at 17°C and finally drops off rapidly to zero at 21½°C.

For the sake of comparison, a representative sample of some writers' results is given in Table III.

TABLE III : The optimum growth temperatures for trout.

Author	Growth Optima (°C)	
Brown (1946)	7- 9	16-19
Crass (1964)		18
Hewitt (1943)		15-19
Pentelow (1939)	10-15	
Swift (1955)	8-12	15-16
Wingfield (1940)	10-15	

Swift's and Brown's figures agree with the graph very well indeed. Hewitt and Crass do not give figures corresponding to the lower peak. This is probably due to the fact that low water temperatures are seldom experienced in the U.S. and Natal during the growing season. Pentelow's and Wingfield's temperatures include the section of figure 8 stretching between the two peaks, so these figures do not agree very well, although it is likely that the figures quoted are merely a rough estimate of the temperatures between which trout grow best.

Frost and Brown (1967) conclude that growth is certainly slow between 7°C and above 19°C. These figures also agree very well with figure 8 and include about 76% of the area under the curve.

It is interesting to note the depression in the growth curve (Figure 8) at a point (12½°C) at which one would intuitively expect a maximum, as indicated. This depression is a modification arising from the activity curve of a trout (See Figure 13) which is maximal in the 10-15°C region and reaches a peak at 13°C. The effect of increased activity at these temperatures is to increase the energy expenditure and therefore decrease the growth rate at temperatures in this region.

The activity curve has another minor peak at 24°C as a result of nervous reaction to the extreme temperature. This peak does not affect the growth rate since food intake falls off to zero and growth is non existent in this region anyway.

To sum up this subsection shows that an excess of food intake over energy expenditure results in growth. Curves representing the change of these two factors with temperature are derived, along with the resultant growth curves and it is found, basically, that with a surplus of food growth improves with temperature up to maximums at about 10°C and at 17°C with an intermediate minimum at 12½°C. This agreed well with evidence from experimental situations but there was no evidence available to confirm or disprove the hypothesis that trout growth would improve with lower temperatures under conditions of a food deficit.

(iii) Death

(a) Death by changes in gas content with temperature.

Like most living organisms, trout require oxygen as a basic essential to life. The physiological process of a fish's breathing is well known, but what is important is that trout can only extract sufficient oxygen from the water, for their needs, if the concentration of the gas is relatively high, relative that is, to the requirements of other fish (See Table IV).

TABLE IV : The minimum concentrations of dissolved oxygen, expressed as a percentage of the saturated value, at which various fish survive at 10°C.

Type	Duration of Test	
	3½ hours	7 days
Rainbow trout	15.3	16.7
Perch	5.8	9.3
Roach	3.2	5.7
Tench	1.9	3.1

Source : Downing and Merkins (1955)

TABLE V : The increasing oxygen requirements of rainbow trout with temperature, expressed as a percentage of the maximum saturated value.

Duration of Test	Temperature of Water 10°C	16°C	20°C
3½ hours	15.3	19.1	23.4
3½ days	16.7	30.2	28.8
7 days	16.7	38.6	29.6

Source : Downing and Merkins (1955)

TABLE VI : Change of solubility of oxygen, carbon dioxide and ammonia, in water, with temperature, expressed as cm^3 of gas at 0°C, and 760 mm mercury, dissolving in $1cm^3$ of water at the stated temperature

Temperature (0°C)	Gas O_2	CO_2	NH_3
0	0.047	1.676	1130
10	0.037	1.163	870
15	0.033	0.988	770
20	0.030	0.848	680
30	0.026	0.625	530

Source : Kaye and Laby (1966)

Table V shows how trout require more oxygen at higher temperatures. There is a minor anomoly in that the figures for required oxygen content are in fact lower at 20°C than at 16°C in the 3½ and 7 day periods. This can be accounted for, again in terms of the activity curve (Figure 13) which shows a minimum at 20°C. This minimum causes a decrease in the rate of energy consumption which in turn leads to a decreasing oxygen intake.

Now, whilst the trout's oxygen requirements rise with increasing temperature, the saturated oxygen content falls with increasing temperature. (See Table VI). Table V also illustrates that trout can survive adverse conditions for a limited period, but succumb if the situation does not improve.

Gases apart from oxygen also affect trout. Carbon dioxide and ammonia dissolved in the water poison trout by impairing the efficiency with which the hoemaglobin of the blood can transport oxygen through the body. At $16\frac{1}{2}^{o}$C rainbow trout can survive an oxygen concentration of as little as 2 parts per million (ppm) provided carbon dioxide is absent, but they die within an hour if the carbon dioxide concentration rises to 15 ppm.

An ammonia concentration of only 1 ppm reduces the amount of oxygen carried by the blood by about 85%.

Although oxygen concentrations decrease with increasing temperature, the rates at which carbon dioxide and ammonia concentrations decrease are about three and two times greater respectively than that for oxygen (See Table VI). The implication is that as temperatures rise, there is progressively less chance of exceeding lethal limits of carbon dioxide and ammonia concentrations.

It must be realised that the values in Table VI are saturated values and in practise these levels of concentration are seldom reached for carbon dioxide and never reached for ammonia, but the mere fact that they are so much more soluble than oxygen means that they will be absorbed that much more readily. In view of this, it is fortunate for trout that there is an abundance of oxygen available for absorbtion from air, whilst the quantities of carbon dioxide and especially ammonia are considerably less. This fact counters the dangerous situation which would arise if all gases were equally available for absorbtion.

The converse of the situation mentioned in the last paragraph but one, is also true so that at low temperatures, although the oxygen concentration might be sufficient, carbon dioxide and ammonia may accumulate to dangerous levels especially in lakes and deep pools on sluggish rivers, where water may stratify by density into thermal layers with little or no vertical convection, except by diurnal heating

close to the surface. Colder water sinks to the bottom where carbon dioxide and ammonia produced by decaying organic matter is readily absorbed with the result that trout forced into this cooler layer by, say, high water temperatures near the surface, may die if the accumulations of carbon dioxide and ammonia are sufficiently high.

Most lakes also have an oxygen deficit in the lower layers because of its use for decay of organic matter, so that there exists an inverse relation between the oxygen and carbon dioxide concentrations in these layers (Hesse 1937).

Of course, the dangerous gases are unlikely to accumulate to dangerous concentrations in swiftly flowing streams since they will be carried away by the current as they are formed, diluted in the entire stream and will not be able to build up to dangerous levels as they can in lower layers of lakes where they are prevented from mixing with the main body of the water. On the other hand, oxygen contents of quickly flowing streams are usually very high due to the presence of rapids, falls and current, which present an enlarged and constantly changing surface for absorbtion of oxygen. Here too, the inverse oxygen to carbon dioxide relationship exists, but it is displaced towards the more favourable side. This also applies to the surface of a lake especially if there is a breeze which ripples the water.

The situation then, is that whilst only very high temperatures are likely to cause trout in streams to die, less high as well as very low temperatures may kill trout in dams, owing to the less effective circulation of water.

In Natal's streams carbon dioxide and ammonia poisoning does not occur because of the factors mentioned above, but a third factor also acts against the accumulation of these gases. This is the geology of the strata from which and over which the rivers flow. The main types

in the trout zone are shown in Table VII.

TABLE VII : The pH and total hardness as calcium carbonate of waters flowing over geological formations in the trout zone.

Formation	pH	Hardness
Stormberg lavas	7.7	52.7
Stormberg sandstone	7.8	50.6
Mid and Upper Beaufort	8.2	39.5
Lower Beaufort	7.6	52.5

Source : (Oliff, 1960)

It is seen that waters in the trout zones are quite hard due to the presence of carbonates and bicarbonates in solution. These buffer the water at a constant pH against the presence of carbon dioxide in the form of carbonic acid and against ammonia in the form of ammonium hydroxide. Now rates of chemical reaction more or less double for a temperature rise of 10^{o}C (vant Hoff's Law) so that this factor reinforces the others as temperatures rise and explains why trout in Natal's streams never die as a result of carbon dioxide and ammonia poisoning.

(b) Death resulting from temperature extremes.

Death resulting from extremes of temperature overlaps largely with the previous subsection owing to the change of gas concentrations with temperature and other circumstances. The emphasis in this subsection however is on the direct effects of temperature on a trout's death, bypassing where possible the effect of changing gas concentraticns.

Trout die, when body fluids freeze, a degree or two below 0^{o}C and also when temperatures rise above (very roughly) 28^{o}C.

It is perhaps necessary to add that the lethal upper temperature limit for trout is very vague and McAfee (1966), amongst others, found it to be dependant on the particular existing permutation of the combined effects of gas content, water temperature, size of the fish, changing

environment situations and acclimatisation. This will be readily accepted in view of previous sections. Rainbow trout in Natal have a greater tolerance of adverse conditions than have brown trout, and under otherwise ideal conditions can survive up to an absolute maximum of $29\frac{3}{4}^{o}C$ for very limited periods.

It is not known why they die at high temperatures (Frost and Brown 1967) but it is possibly due to respiratory failure because of the low oxygen content or due to some other physiological change.

All trout die at $0^{o}C$ but the less well defined upper limit may be extended by a period of acclimatisation (See Table VIII). Exposure to high temperatures has an accumulative effect unless there is a period of recovery for many hours at a temperature lower than $21^{o}C$.

TABLE VIII : Effect of acclimatisation on the survival of trout. Temperatures are given in ^{o}C and are the maximum temperatures at which half the trout survived for the stated period.

Acclimatisation Temperature ^{o}C	Duration of Test 12 hrs.	24 hrs.	48 hrs.	7 days
5	22.5	22.5	22.5	22.5
10	24.5	24.2	24.2	24.2
15	26.2	25.6	25.1	24.5
20	26.5	26.3	25.8	24.8
23	27.8	26.8	26.4	25.3

Source : Frost and Brown (1967)

Note: Acclimatisation temperature is that temperature at which the trout have been living for at least two days.

Death by temperature extremes does occur every so often in Natal and corresponds to a period of sustained drought in summer. Rivers shrink to a mere trickle connecting a series of small pools in which the trout are forced to congregate. In this situation, everything acts against the trout. The concentrated trout population use up oxygen and produce carbon dioxide and ammonia. The balance of gas is not quickly restored due to the poor flow of the stream and, apart from this, the smaller the

pool becomes, the shallower it gets and the more it retreats from the protective shade of the marginal vegatation so that is responds much more quickly to a hot day with a large temperature rise.

Although trout can survive a range of temperatures from $0^{o}C$ to about $28^{o}C$ they are susceptible to a very severe change of temperature if the rate of change is so abrupt that no conditioning can occur.

It is because of this that trout survive heavy winter snowfalls, but succumb to a mid summer hailstorm, since in winter water temperatures are low anyway and the snow has little additional effect, whereas warm water in summer can be suddenly chilled by a heavy hailstorm.

To kill trout, however, the temperature change must be very violent and Crass (1970) found that a temperature drop from $25.5^{o}C$ to $6^{o}C$ in less than an hour after a hailstorm failed to kill trout in the Mooi River.

Less fortunate were the trout in the Loteni River which were killed in their thousands by a vicious hailstorm and resulting flood in December 1954. The abrupt temperature drop paralyses the fish which are then washed away by the river or left stranded on the banks.

The opposite extreme, of an abrupt temperature rise does not occur under natural conditions and although water temperature may rise considerably during a hot spell, the rate of change cannot compare with that following a hailstorm. For example on a very hot day (27/2/65) the Bushmans River at the confluence with the Ncibidwane the water temperature rose from $18.5^{o}C$ at 11 am to $24^{o}C$ at 3 pm. Compared to the figures given for the Mooi River this situation took four times as long to give a temperature change only a quarter as large.

In streams in Natal then, trout die not because of low temperatures, but because of sustained high temperatures or because of sudden temperature drops.

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18 Aug 1971

Professor O.W. Williams

Dear Professor,

I have read the Undergraduate Thesis by G.D. Peckham on the effects of temperature on trout.

I consider that he has made good use of the available literature to present a well-correlated account, and has also exhibited an ability to think things out for himself.

I have no serious criticisms of the subject matter, & would indeed commend his efforts both for presentation & content.

Yours sincerely,

Robert Crass